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# Induction of *Zugunruhe* by Photostimulation of Encephalic Receptors in White-Crowned Sparrows


Abstract. *Daily 20-hour encephalic photophases (DEPP), transmitted (hours 0 to 20) via chronically implanted light-conducting fibers to selected sites in the basal hypothalamus of male white-crowned sparrows, were superimposed on daily 8-hour (hours 0 to 8) external ambient photophases (DAPP). Initially the birds displayed motor activity only during the 8-hour DAPP. After a delay of at least 2 weeks, some of the birds became intensively active during hours 8 to 20. We postulate that this period of "nocturnal" activity is equivalent to the nocturnal* Zugunruhe *shown by caged individuals of many nocturnally migratory species subjected to long days; such activity is generally regarded as the expression of migratory behavior.*


It is well known that day length is the primary environmental information in the control of the annual cycles of many species of birds (*1*). Experiments with bilaterally enucleated birds have demonstrated that eyes are not necessary for the perception of light in the photoperiodic induction of gonadal development in several species (*2*). In *Passer domesticus* (house sparrow) extraretinal photoreception is also involved in the entrainment of circadian locomotor rhythms (*3*). The extraretinal photoreceptors in the photoperiodic gonadal response in the domestic mallard (*4*), Japanese quail (*5*), and house sparrow (*6*) are localized in the brain, and in the first two, specifically in the hypothalamus. In the house sparrow the extraretinal photoreceptors that entrain circadian rhythms are also encephalic (*7*).

To locate the extraretinal photoreceptors involved in the photoperiodically induced testicular growth of the highly photoperiodic, migratory white-crowned sparrow, *Zonotrichia leucophrys gambelii*, we devised a scheme (*8*) for introducing a minute light source into selected encephalic sites in the brains of relatively unrestrained birds by the use of light-conducting fibers. Two light-conducting fibers are used. The first is plastic (Crofon, Du Pont) and is about 0.25 mm in diameter and 20 cm long. This fiber is coiled to permit movement by the bird; it conducts light from an incandescent lamp to a second fiber of rigid glass (Corning) that is about 0.05 mm in diameter and 7 to 13 mm in length and is ensheathed with stainless steel tubing so that light leaves only from its very distal end. This second fiber conducts light from the plastic fiber to the selected encephalic site. The rate of emission of light from the end of the glass fiber into the brain tissue is of the order of $10^{-4}$ $\mu$W for the range $\lambda$ = 400 to 700 nm.

We have found that the direct illumination of the ventromedial and tuberal hypothalamic regions for 20 hours per day induces testicular growth in both intact and bilaterally enucleated white-crowned sparrows; this growth may be as rapid as that induced by an ambient daily photophase of the same duration (*8*). We describe here the effect of 20-hour daily photophases (DEPP) delivered directly to hypothalamic and adjacent areas, and superimposed on an 8-hour daily ambient photophase (DAPP), on the temporal pattern of perch-hopping in white-crowned sparrows.

Male white-crowned sparrows were placed individually in cages (22 by 13 by 22 cm) with a perch that activated a recording microswitch so that motor activity could be monitored. Ambient illumination (DAPP) was provided with two 50-W incandescent lamps housed in reflectors to provide an intensity of 3 to 10 lux at perch level. The birds were neither visually nor acoustically isolated from each other. Light-conducting fibers were inserted stereotaxically into selected sites in the brains of males that had been held on a short-day regime [8 hours of light and 16 hours of darkness (8L:16D)] for 8 months, and were, therefore, highly photosensitive. On the day after insertion of the fibers a photoperiodic regime of 20L:4D (DEPP) was initiated through the fibers. Initially a neutral-density filter with 10 percent transmittance (9) was inserted between the lamp and the proximal end of the plastic light-conducting fiber. Illumination in the chamber was continued at 8L:16D (DAPP) with "light on" (hour 0) coincident with "light on" of DEPP. For comparison with maximum responses a group of six birds was transferred to another chamber in which they were subjected to 20L:4D ambient illumination of at least 400 lux. Exploratory laparotomies were performed to estimate testicular weight (10), before implantation of the fibers and at approximately 2-week intervals after the onset of DEPP. The neutral-density filter was removed from the system of those birds that had not shown appreciable testicular growth at the first laparotomy on day 18, a tenfold increase in light intensity thus being attained. After 46 days of photostimulation via light-conducting fibers birds were killed. The testes were weighed after fixation and then examined histologically for spermatogenic activity. Brain sections were examined to verify the sites of the tips of the implanted light-conducting fibers (11).

Of 24 males stimulated via implanted light-conducting fibers and for which we obtained adequate records of motor activity, 11 (implanted respondents, FO-R group) showed appreciable testicular growth with estimated testicular growth-rate constants $k$ (12) of 0.026 to 0.090 (median, 0.046), and spermatogenic activity. In the implanted nonrespondents (FO-NR group) there was no appreciable testicular growth or spermatogenesis except in two birds in which there was slight growth of testes and activation of spermatogenesis. Eight of 11 FO-R birds developed motor activity during hours 8 to 20 (time of DAPP "lights off" and DEPP "lights on"), beginning 13 to 35 days after the onset of DEPP (Fig. 1). The intensity of this activity was comparable to, or at times greater than, that of the activity during DAPP (hours 0 to 8). In most cases the onset of this activity was preceded by a pause of about 1 hour after the cessation of activity at the end of DAPP, and ceased before or, more frequently, at the end of DEPP at hour 20. During hours 20 to 24 there was no perch-hopping except occasional anticipatory activity preceding the simultaneous onset of DEPP and DAPP at hour 0. Two of the 13 FO-NR birds developed perch-hopping during hours 8 to 20. These were the two that showed a slight

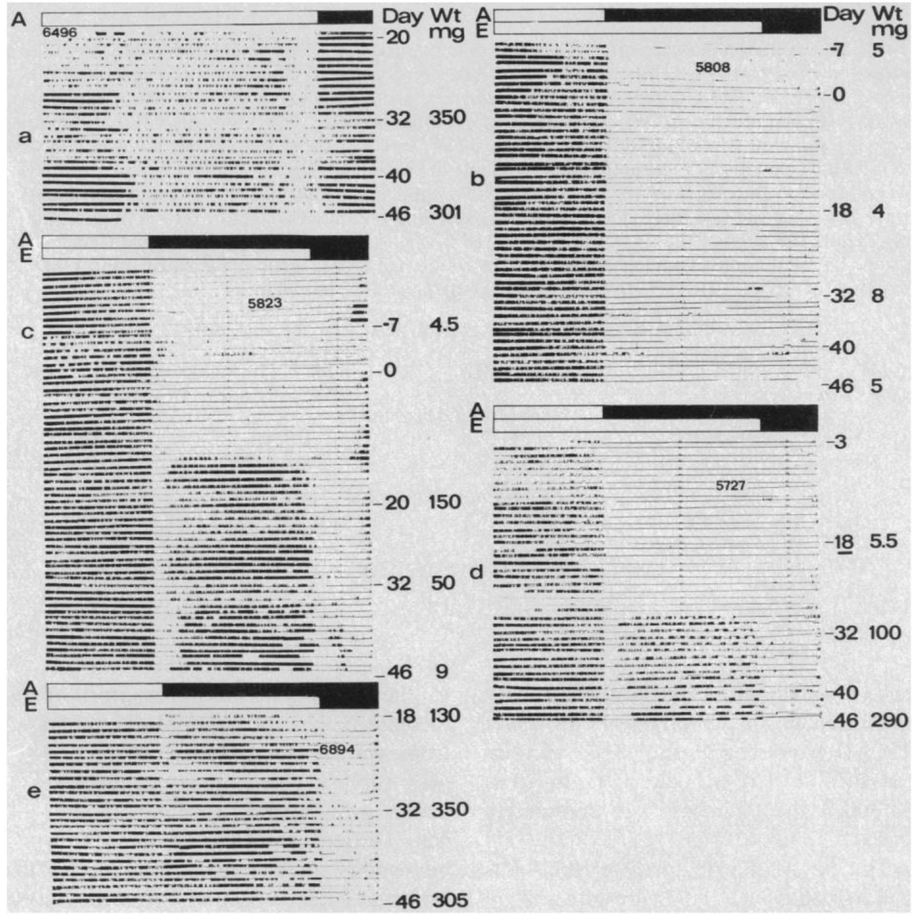


Fig. 1. Examples of the effect of DEPP on the pattern of locomotor activity (perch hopping) in male white-crowned sparrows. Horizontal lines display perch hopping on successive days, top to bottom, beginning with the onset of the daily 8-hour DAPP at hour 0. Bars above day 1 of recording indicate the times of DAPP (*A*) and DEPP (*E*). Days before or after onset of DEPP and measuring of testicular weights are recorded in the right margin; the final recorded weight was obtained by actual weighing; others are estimates from laparotomies (10). In all cases the light-conducting fibers were installed on day −1. (a) Intact long-day control (6496). Activity recording began on day 19, by which time the bird had already developed intense *Zugunruhe* during the 4-hour environmental scotophase. On day −7, the CTW was 5 mg; on day 18 it was 180 mg. This record is typical of the long-day controls. (b) Effect of DEPP on perch-hopping of a bird (5808) that showed no photoperiodic testicular response. The tip of the implanted fiber was in the ventromedial hypothalamus. Perch-hopping occurred exclusively during the 8-hour DAPP. This record is typical of fiber-implanted birds that did not develop *Zugunruhe*. (c) Effect of DEPP on perch-hopping of a bird (5823) with pronounced photoperiodic testicular response (estimated maximum $k = 0.085$). The tip of the light-conducting fiber was in the lateral aspect of the infundibular nucleus. Perch-hopping during hours 8 to 20 began on day 13. Although testis weight declined after reaching an estimated 150 mg on day 20, apparently because of a defect in the light-conducting system, the pattern of extended activity persisted with the precise timing of its offset at hour 20 unchanged. The persistence of this activity in the presumed absence of light during hours 8 to 20 is not unexpected, because in white-throated sparrows *Zugunruhe* persists for a considerable period of time after release into continuous dim light (13). A second bird (6881; also apparently with a defect in the fiber system), in which testicular growth to an estimated 120 mg on day 32 was followed by a decrease in weight, had a very similar perch-hopping record. Note that the onset of activity during hours 8 to 20 was preceded by a pause of 1 to 2 hours after the termination of daytime activity. This is consistent with the perch-hopping recorded for this species under its natural vernal photoperiodic regime (16). (d) Effect of DEPP on perch-hopping of a bird (5727) that showed testicular growth only after a tenfold increase in intensity of DEPP (estimated maximum $k = 0.074$). On day −7, CTW was 2.5 mg. The tip of the light-conducting fiber was in the oculomotor nerve immediately posterior to the infundibular nucleus. Activity recording began on day 3. On day 18 the neutral density filter was removed, thus causing a tenfold increase in the intensity of the transmitted light. Note the virtual lack of testicular growth before day 18 and marked growth thereafter. There is a pause between two phases of perch-hopping. This is similar to the other birds (with implanted fibers) in the presence of a rest period between the end of daytime activity and the beginning of *Zugunruhe*. (e) Effect of DEPP on perch-hopping of a bird (6894) that showed testicular growth (estimated maximum $k = 0.074$). The tip of the implanted fiber was in the optic chiasma adjacent to the ventromedial hypothalamus. Activity recording began on day 18 after *Zugunruhe* had already begun. The intensity and duration of this activity on day 18 were doubtless suppressed because of the laparotomy performed earlier on the same day. This bird is exceptional in that there was no pause between the two periods of activity. Note in (c) to (e) the precision of the termination of *Zugunruhe* at hour 20, and the lack of perch hopping during hours 20 to 24.

Table 1. Correlation between sites of the tips of implanted light-conducting fibers with testicular growth and extended perch-hopping activity (*Zugunruhe*) in 20 white-crowned sparrows subjected to DEPP. The ten birds with *Zugunruhe* are grouped according to the estimated combined testicular weight (CTW) at the onset of extended activity. The ten birds without *Zugunruhe* are grouped according to the maximum CTW, and only those individuals for which more than 25 days of activity recordings were available are included. The estimated testicular weights were obtained by extra- or intrapolation of all weight data. The maximum testicular weights were largest of the last three measurements, excluding the initial weights. Letters in parentheses denote the sites of the tips of the implanted fibers: AH, anterior hypothalamus; Cer, cerebrum; IN, infundibular nucleus; ME, median eminence; OC/T, optic chiasma or tract; OMN, oculomotor nerve; PD, pars distalis; VMH, ventromedial hypothalamus.

| Number of individuals in range of testicular weight (mg) | | | | |
|---|---|---|---|---|
| CTW < 10 | 10 < CTW < 20 | 20 < CTW < 50 | 50 < CTW < 100 | 100 < CTW |
| | | *Birds with* Zugunruhe | | |
| 1 (AH) | 1 (IN) | 1 (IN) | 1 (IN) | 1 (OC/T) |
| 1 (IN) | 1 (Cer) | 1 (OC/T) | 1 (OMN) | 1 (OMN) |
| | | *Birds without* Zugunruhe | | |
| 3 (AH) | 1 (VMH) | 1 (OC/T) | | 1 (OC/T) |
| 2 (VMH) | | | | |
| 1 (ME) | | | | |
| 1 (PD) | | | | |

testicular response. By the time activity recording was begun on day 19 the intact 20L:4D group had already developed intense *Zugunruhe* (*13*) during hours 20 to 24 when the chamber was completely dark (Fig. 1a).

The tips of the majority of the light-conducting fibers that were effective in the photoperiodic induction of testicular growth or extended locomotor activity were located in the infundibular nucleus, ventromedial hypothalamus, and optic chiasma–optic tract, or oculomotor nerve, immediately adjacent to the first two areas, with exceptions of one implant each in the anterior hypothalamus and ventroposterior aspect of the cerebrum (Table 1). From analyses of a larger number of birds in which testicular growth was stimulated through implanted light-conducting fibers (*8*), we think that the infundibular nucleus and possibly ventromedial hypothalamus are the foci of photosensitivity and that light from the tips of fibers that are located more dorsally or adjacent to these areas was stimulatory because of transmission through tissue to the areas of the infundibular nucleus and ventromedial hypothalamus.

That activity during hours 8 to 20 began only with some delay after the onset of DEPP indicates that it was not a direct motor response to DEPP. If such had been the case, activity would have been expected from hour 0 to 20 from the first day of administration of DEPP. Moreover, the fact that the majority of the birds that eventually developed activity during hours 8 to 20 showed a clear indication of testicular growth and development (Table 1) suggests that the direct administration of long daily photophases to the encephalic photoreceptors that mediate release of hypophysial gonadotropin induces increased secretion of gonadotropins, which, in turn, induce testicular growth and secretion of androgen. Testicular androgens, in turn, may be responsible for release of hypophysial prolactin, thus creating the necessary hormonal environment for the development of vernal premigratory and migratory behavior, *Zugunruhe* (*14*). This would explain the delayed onset of perch-hopping during hours 8 to 20. The interpretation of the activity during hours 8 to 20 as *Zugunruhe* appears, at least superficially, to be inconsistent with the behavior of the 20L:4D group. Whereas in the latter, *Zugunruhe* occurred in total darkness, it was restricted to the time of DEPP in the encephalically illuminated birds with almost no activity in total darkness, hours 20 to 24. Although this question cannot be resolved with the data at hand, it should be noted that *Zugunruhe* in several species (*15*) is greatly reduced or inhibited when darkness in the L:D cycle is total darkness rather than very dim light. We therefore raise the possibility that DEPP had the effect of dim environmental light with respect to the time of expression of *Zugunruhe*, so that it was almost entirely restricted to hours 8 to 20. Had DEPP exerted the effect of bright environmental light, motor activity should have occurred during hours 8 to 20 immediately after the onset of DEPP as in the group that was transferred from 8L:16D to 20L:4D environmental light.

This experiment demonstrates that direct stimulation of encephalic receptors in the basal hypothalamus, and perhaps in adjacent areas, induces, after a delay of at least 2 weeks, a pattern of "nocturnal activity." Because the development of this pattern is very similar to that of the development of that of a vernal type of *Zugunruhe* in intact white-crowned sparrows that have experienced a change from short days to long days, and because of the similarity of its temporal relation to the development of the testes with that of photoperiodically induced *Zugunruhe*, whether natural or experimental (*13, 14, 16*), we think that this activity is the physiologic and behavioral equivalent of vernal *Zugunruhe*. Our results also confirm that an extended period of motor activity per se is neither a prerequisite nor an essential concomitant for testicular growth, because the majority of birds that developed *Zugunruhe* had already undergone the initial phase of testicular growth (Table 1) while their activity was restricted to the 8-hour DAPP. In addition, three birds did not develop *Zugunruhe* despite clear signs of testicular stimulation; this can be explained either by inadequate durations of activity recording or by the empirical observation that not all photostimulated white-crowned sparrows develop measurable *Zugunruhe*.

Under conventional photostimulatory conditions gonadal growth is associated with a long daily phase of locomotor activity corresponding with the long daily photophase. To our knowledge this is the first demonstration that stimulatory long photophases, as far as testicular growth is concerned, can occur with an activity pattern typical of nonstimulatory short days, which is consistent with the results of earlier investigations in which males of this species were subjected to "asymmetric skeletons" of long days (*17*).

Since we used nonstimulatory short daily environmental photophases instead of constant darkness as the ambient photoperiodic regimen, we do not know the effects of L:D cycles delivered solely to the encephalic photoreceptor on the pattern of locomotor rhythms. However, it should be possible to entrain "daytime" activity in this species by this means, if the white-crowned sparrow is similar to the house sparrow with regard to the involvement of encephalic photoreceptors in entrainment of the circadian cycle of locomotor activity. Also, our use of a nocturnal migrant may have complicated the interpretation of the results because of the development of the second type of locomotor activity, that is, *Zugunruhe*. However, this may have been fortuitous because, without the development of *Zugunruhe*, we may not have seen changes in activity patterns in birds under treatment with DEPP. Further experiments of this type on both migratory and nonmigratory species might help to answer the questions raised here as well as others concerning important aspects of avian encephalic photoreceptors.

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9. Kodak Wratten gelatin gray neutral density filter with 10 percent transmittance.
10. The left testis was exposed by a small incision made between the last two ribs and compared with a series of preserved, previously weighed pairs of testes; the combined weight was then estimated. The error of this method is ± 20 percent between combined testis weights of 20 to 200 mg and tends to be greater outside this range.
11. In experiments with several groups of controls (*8*), we illuminated encephalic sites with the same light-conducting units and measured testicular growth and, in some cases, plasma levels of luteinizing hormone and testosterone, but we did not record motor activity. One group consisted of bilaterally enucleated birds with implanted light-conducting fibers, another group consisted of bilaterally enucleated birds with "blank" implants, that is, units without light-conducting fibers and with or without light sources, and another group consisted of intact birds with blank implants. Results from these groups demonstrated that the responses are independent of the eyes and that they are not induced by mechanical effects of the units or by injuries inflicted during their implantation.
12. In white-crowned sparrows, photostimulated testicular growth is a log-linear function of time until combined weight reaches about 200 mg [for calculation of the logarithmic testicular growth-rate constant, $k$, see D. S. Farner and A. C. Wilson, *Biol. Bull.* **113**, 254 (1957)]. Estimates of maximum testicular growth rates were obtained by taking the larger of the two estimated $k$ values for each bird, $k_{0-18}$ or $k_{18-32}$, the former being the estimate of testicular growth rate for days 0 to 18 and the latter for days 18 to 32. The maximum rate of testicular growth obtainable with 20L:4D cycles in this species is approximately 0.090. In this experiment the estimated $k$ for the six intact birds on 20L:4D was 0.089.
13. Caged photosensitive white-crowned sparrows when photostimulated by long daily photophases develop intense nocturnal activity, *Zugunruhe*, which is regarded as an expression of vernal nocturnal migratory flight [D. S. Farner, L. R. Mewaldt, J. R. King, *J. Comp. Physiol. Psychol.* **47**, 148 (1954)]. *Zugunruhe* has been used routinely as an indicator of migratory behavior in experimental investigations [H. O. Wagner, *Z. Vergl. Physiol.* **12**, 703 (1930); V. R. Dolnik, *Migratsionnoe Sostoyanie Ptits* (Akademiya Nauk SSSR, Moscow, 1975), pp. 116–137; P. Berthold, in *Grundriss der Vogelzugskunde*, E. Schüz, Ed. (Parey, Berlin-Hamburg, 1971), p. 257].
14. Results of experiments involving administration of exogenous hormones and hypothalamic lesions in this and related species indicate that photoperiodic induction of vernal premigratory fattening and vernal *Zugunruhe* is mediated by adrenohypophysial, gonadal, and possibly adrenal hormones [A. H. Meier and D. S. Farner, *Gen. Comp. Endocrinol.* **4**, 584 (1964); ———, J. R. King, *Anim. Behav.* **13**, 453 (1965); A. H. Meier and D. D. Martin, *Gen. Comp. Endocrinol.* **17**, 311 (1971); A. H. Meier, in *Proceedings of the 16th International Ornithological Congress*, H. J. Frith and J. H. Calaby, Eds. (Australian Academy of Science, Canberra, 1976), p. 355; K. Yokoyama, *Cell Tissue Res.* **174**, 391 (1976)]. In white-crowned sparrows under a regimen of 16L:8D *Zugunruhe* began after 15 to 20 days when the combined weight of the testes reached 50 to 100 mg [K. Yokoyama, thesis, University of Washington (1975)].
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17. D. S. Farner, R. S. Donham, R. A. Lewis, unpublished results. In these experiments the 18-hour daily scotophase was interrupted with a 2-hour secondary photophase at times that induced significant growth of the testes. Until the onset of *Zugunruhe*, 15 to 20 days after initiation of the regime, growth of the testes occurred, whereas motor activity was largely restricted to the 6-hour and 2-hour photophases.
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## Anxiety Change Through Electroencephalographic Alpha Feedback Seen Only in High Anxiety Subjects

Abstract. *Subjects who were either high or low in trait anxiety used alpha feedback to increase and to decrease their electroencephalographic alpha activity. The alpha changes were tightly linked to anxiety changes, but only in high anxiety subjects (for whom anxiety was reduced in proportion to alpha increases, and was increased in proportion to alpha suppression). Low trait-anxiety subjects were superior at both enhancement and suppression training, but their alpha changes were not related to anxiety changes. In both groups, anxiety changes were generally unrelated to either resting levels or changes in frontalis electromyograms and respiration rate. These results suggest that long-term alpha feedback training (at least 5 hours) may be useful in anxiety therapy.*

Recently, Orne and Paskewitz (*1*) reported "a lack of the expected relationship between alpha density and the apprehension, anxiety, fear, or arousal level of the subjects" (*1*, p. 460). This paradoxical outcome, counter to 35 years of electroencephalographic (EEG) research (*2*), was interpreted to cast doubt on the "expected" inverse alpha anxiety relationship, and to "challenge the widely accepted rationale for using alpha feedback training as a means of teaching individuals control . . . of anxiety."

However, several methodological problems and unproved assumptions weaken their challenge to the use of learned alpha increases for anxiety. Orne and Paskewitz (*1*) did not select high anxiety subjects; in fact they probably eliminated them by excluding subjects with low alpha levels and subjects afraid of electric shock. Instead, they sought to increase anxiety (by threat of electric shock) and then to measure alpha changes. Anxiety levels were never directly measured and no attempt was made to measure alpha changes accompanying reduced anxiety. Orne and Paskewitz reasoned backward from their anxiety manipulations to conclusions about possible effects of alpha manipulations (that is, through feedback). Their reasoning assumed a symmetric relation between alpha activity and anxiety. However, nonsymmetric relations are common. Thus (absent symmetry) shock-induced increases in anxiety could fail to affect alpha as reported (*1*) and yet feedback-induced alpha increases could still effect anxiety reductions.

The problem in anxiety therapy is to reduce, not increase, anxiety, so we trained both high and low trait-anxiety people to control the amount of alpha activity (8 to 13 Hz) in their brain waves. Occurrence of EEG alpha activity sounded a tone whose loudness was proportional to the instantaneous alpha voltage. Volunteers for alpha feedback training (100 college males) were paid $1.50 to take the Minnesota Multiphasic Person-


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